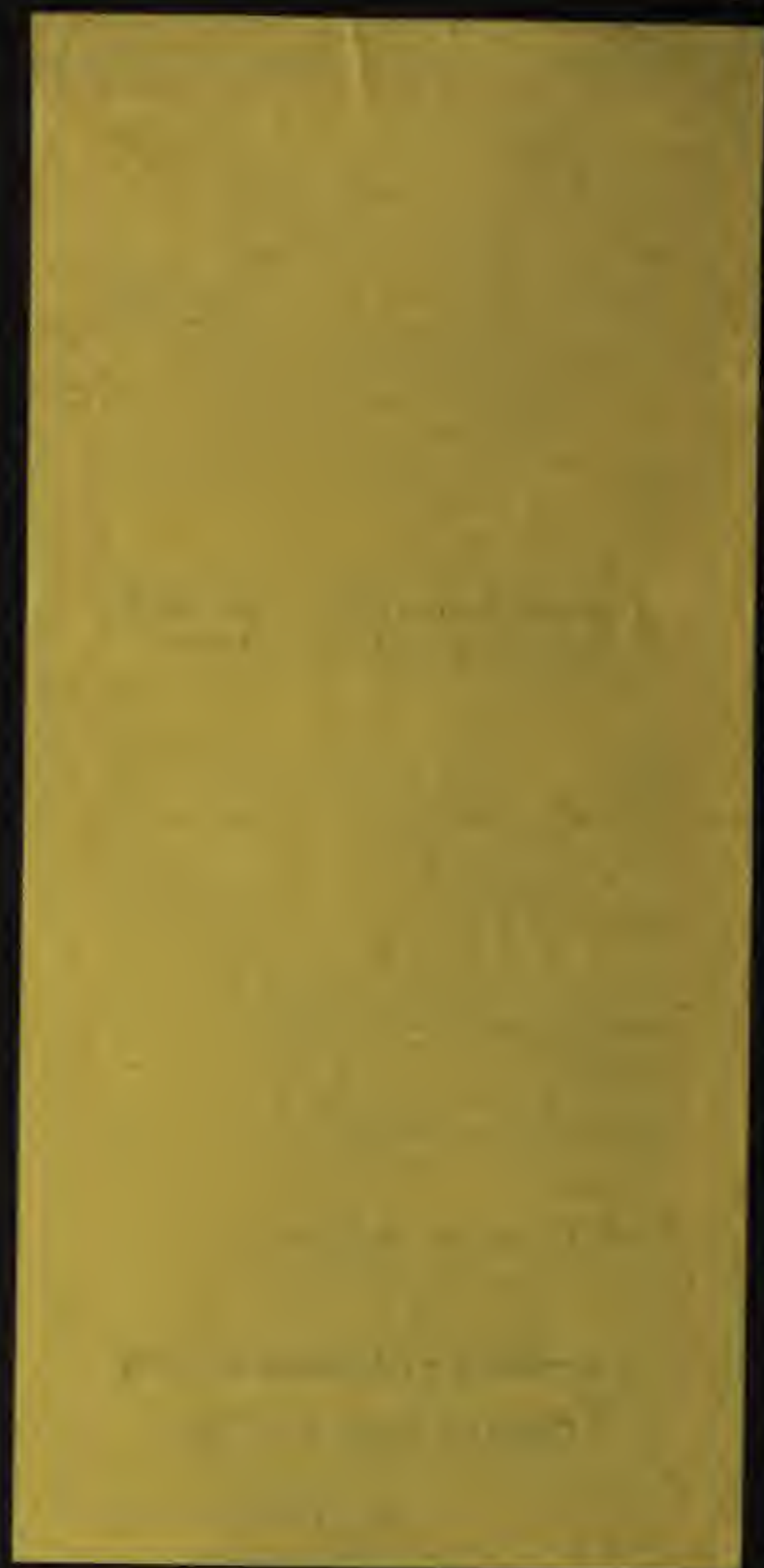


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BY

WILLIAM H. WESTON, JR.

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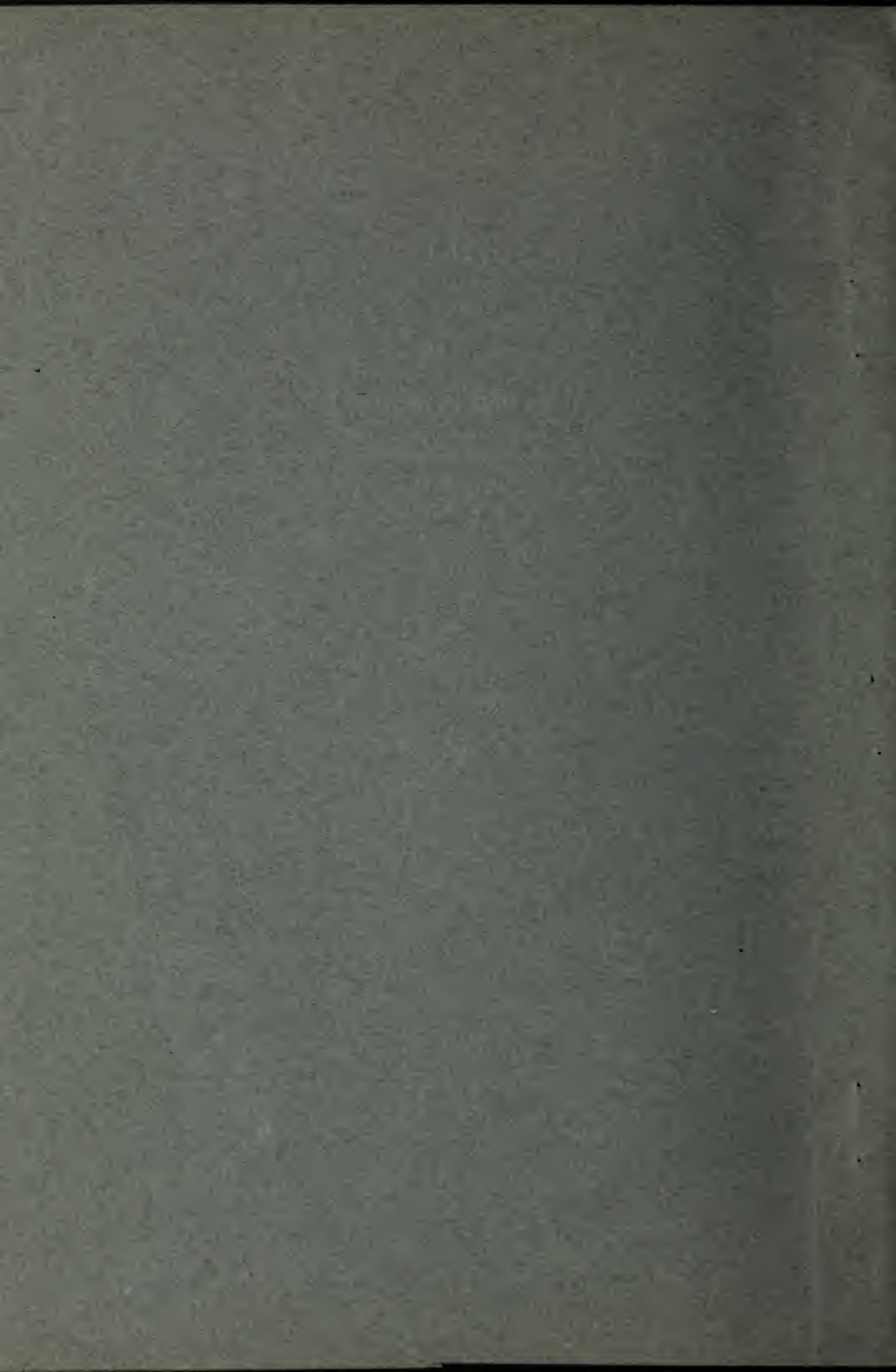
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## ANOTHER CONIDIAL SCLEROSPORA OF PHILIPPINE MAIZE

By WILLIAM H. WESTON, JR.

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Each year in the Philippine Islands the valuable maize crop suffers very severe losses from the destructive activities of downy mildew (*Sclerospora* spp.). While the writer was studying this disease during the past two years his attention was naturally directed to the question whether the widespread destruction of maize throughout the thousand-mile extent of these scattered islands was due in all cases to the same species of fungus. A comparative study of material collected from many parts of the provinces of Batangas, Laguna, and Rizal in the island of Luzon, where the disease is most serious and where it was studied most intimately, showed that in all cases the same causal fungus was involved. This species of downy mildew was described in an earlier paper (12)<sup>1</sup> as *Sclerospora philippinensis*. It was only natural to suspect that some of the abundant Philippine wild grasses related more or less closely to maize would be found to harbor this or other *Sclerosporas*. As on the widely distributed wild grass *Saccharum spontaneum* L. (Pl. 77, A) the oogonial stage of a *Sclerospora* had been very commonly encountered in great abundance, this grass was obviously an object of suspicion. In Luzon, however, despite extensive search, no conidial stage was seen on this host.

During a trip to the more southern Visayan Islands of Cebu, Bohol, and Leyte, in which maize is a crop of very great importance, the writer found that there, also, the maize plantings were suffering heavy losses from downy mildew. As no microscope was carried, no study of the causal organism was made at night during the period of conidium production. However, inasmuch as the symptoms and the general effect of the downy mildew were the same in these southern islands, the writer inferred that the causal organism was that which he had found so widely distributed on maize throughout the northern island of Luzon. Also the wild grasses of these southern islands were carefully examined as possible

<sup>1</sup> Reference is made by number (italic) to "Literature cited," p. 684.

hosts for downy mildew. After long search a clump of bugan̄ grass (*Saccharum spontaneum*) heavily infected by a conidial *Sclerospora* was discovered by Mrs. Weston. Continued hunting brought the fungus to light on the same host in two other places, all three cases being encountered in the rugged interior uplands of Cebu (Pl. 76), which lie between Carcar and Barili. In the island of Leyte, also, this *Sclerospora* was again found on bugan̄ grass on a hillside about three miles from Baybay. No other cases of downy mildew either on this or on other hosts were seen. Later, in a field of native sugar cane near Guadelupe cemetery outside the town of Cebu, a single clump of cane was found infected with the conidial stage of a *Sclerospora*.

The infected plants of *Saccharum spontaneum* and sugar cane were transplanted to Los Baños, Luzon, for further study (Pl. 77, B). There a comparison of living material taken from these plants during the optimum time of nocturnal conidiophore production showed that this downy mildew from the southern islands was different from that previously studied in Luzon. This discovery necessitated a revision of all available material in order to determine whether or not other forms had been previously overlooked under the assumption that the collections were all of the same form so commonly found in Luzon. Accordingly, living material from maize, teosinte, and sorghum from the college plots and from native fields in Batangas and Laguna provinces was compared with the living material from the plants of *Saccharum spontaneum* and sugar cane brought from Cebu. Dried, preserved, and mounted specimens from maize collected in various parts of Luzon were compared with similar specimens from maize obtained in various localities in Cebu, Bohol, and Leyte. This survey showed clearly that all the material so far encountered fell into one or the other of two distinct species—one, the form with shorter, broader conidia found on maize, etc., in Luzon and previously described as *Sclerospora philippinensis*, and the other, which will be called *Sclerospora spontanea*, characterized by longer, narrower conidia, and found on maize, bugan̄ grass, and sugar cane in the Visayas. Once this point had been established, a comprehensive study was made of the two species to determine the resemblances and differences between them in morphological and physiological characteristics.

#### COMPARATIVE STUDY OF SCLEROSPORA PHILIPPINENSIS AND SCLEROSPORA SPONTANEA

##### FIELD CHARACTERISTICS

On maize, as observed in the field in the more southern islands and in Luzon, the two species are apparently identical in their destructiveness to the crop as a whole and also in their effect on the individual plants. It is possible that quantitative studies of essentially similar fields infected by the separate species would show some slight differences, but in general appearance there is no distinction whatever between the two.

## PHYSIOLOGICAL CHARACTERISTICS

Several varieties of maize grown in sterile soil and under controlled conditions preventing contamination were infected with spores produced on the living plants of bugan̄ grass (*Saccharum spontaneum*) and sugar cane brought from Cebu. Parallel inoculations were made also with *Sclerospora philippinensis*. No difference was apparent either in symptoms or in the virulence of the resulting infection. Similar experiments with seedlings of cultivated wheat, *Setaria*, *Pennisetum*, and several species of wild grasses, including the very common aguin̄ay (*Rottboellia exaltata* L.), anias (*Andropogon sorghum* var. *halepense* L.), cogon (*Imperata cylindracea* L.), and tigbee (*Coix lachryma-jobi* L.), using the long, narrow conidia of the southern species, were as uniformly unsuccessful as they had been with *Sclerospora philippinensis* (12). Seedlings of teosinte (*Euchlaena luxurians* Schrad.) and the wild grasses, *Saccharum spontaneum* and *Miscanthus japonicus* (Thunb.) Anders., were successfully inoculated with both forms. No seeds of sugar cane were available for planting. Had there been, there is little doubt in the mind of the writer that infections in this case also could have been obtained. A more detailed account of these inoculation experiments will be given in a later paper. It should be said here, however, that the effect of the *Sclerosporas* varied with the different hosts, being most destructive on maize and least so on bugan̄ grass; but the characteristic production of conidiophores took place with uniform regularity at night on all (Pl. 78, B).

A comparative study of material of *Sclerospora spontanea* on these different hosts showed that the distinguishing morphological characteristics of the fungus had not been altered in any way. Moreover, even after transition from one host to another through several generations, the species remained constant and in no way approached *S. philippinensis*. In like manner, after inoculating various hosts and passing through several generations, *S. philippinensis* also was quite unchanged and showed no tendency to approach the long-spored form.

The writer considers it quite possible that an exact statistical study of large numbers of individuals infected by each of the two fungi would reveal some slight quantitative difference in the area bearing conidia, or in the rate of growth of hyphae through the host, or in some other aspect not at once apparent to an ordinary comparative examination. It should be noted here, however, that there is certainly no noticeable physiologic difference between the two in virulence, range of hosts, or general course of the resulting disease they produce.

## MORPHOLOGICAL CHARACTERISTICS

Therefore, because the two forms differ morphologically rather than physiologically, they were carefully compared in order to determine whether the points of difference were sufficiently stable and well marked

to establish the long-spored form as a species distinct from *Sclerospora philippinensis*.

MYCELIUM.—In morphological characteristics, extent, and relation to the host tissue, the mycelium of the two fungi showed no distinctions sufficiently marked or unvarying to warrant their use as a basis of separation. However, the club-shaped hyphae (conidiophore initials) which grow out through the stomata and develop into conidiophores are different in the two forms, those of the long-spored *Sclerospora* being markedly longer, more slender, and more irregular.

CONIDIOPHORES.—In general appearance the conidiophores of the two *Sclerosporas* are noticeably dissimilar, those of the Visayan form being markedly longer, more slender, and more spreadingly branched than those of *Sclerospora philippinensis*. On analyzing this dissimilarity the details of difference discussed in the following paragraphs are apparent.

The basal cell of the Visayan *Sclerospora* is very long (Pl. 79, A, D, E, F, H), strikingly longer than that of *Sclerospora philippinensis*. The length (140 to 260  $\mu$ ) is greater not only actually but also relatively, for even in the unusual cases when it is less conspicuously long (Pl. 79, G) the basal cell of the Visayan *Sclerospora* always exceeds or at least equals in length that part of the main axis extending from the terminal septum of the basal cell to the origin of the primary branches. In *S. philippinensis*, the basal cell is always shorter than this part of the main axis. Moreover, the basal cell of the Visayan *Sclerospora* is much more slender, usually 5 to 8  $\mu$  at its narrowest diameter, and much less knobbed or swollen at its base (Pl. 79, A, D, E, F, H) than is the basal cell of *S. philippinensis*.

The main axis of the Visayan *Sclerospora* expands more abruptly above the basal cell and then constricts more distinctly (Pl. 79, A, D) just below the branches than in *Sclerospora philippinensis*. The greatest diameter (22 to 32  $\mu$ ), which usually slightly exceeds that of *S. philippinensis*, is thus placed, not just below the branches (as in *S. philippinensis*), but some distance lower (Pl. 79, A, D, G, H).

The branches of the Visayan form generally are less constricted at their point of origin, are of more uniform diameter, and are straighter, less ascending, more spreading, and do not recurve, but stand out from the main axis more stiffly. They are characteristically longer and more slender, but, even if short and crowded, they stand out more stiffly than in *Sclerospora philippinensis*. Although varying considerably in both species, the number of conidia produced on conidiophores is approximately the same in *S. spontanea* and in *S. philippinensis*. In the former, 32 to 48 are commonly borne, although as many as 88 or as few as 12 may less frequently occur.

The sterigmata also are straighter, less recurved, and stand out more stiffly than in *Sclerospora philippinensis*, and, usually they are longer (about 13  $\mu$ ). It should be noted, however, that the length varies with

the extent of the branch system, since in cases where this is reduced and the primary branches or even the main axis give rise directly to sterigmata, these sterigmata are much larger (Pl 79, B) than they are when arising from quaternary or tertiary branches as the ultimate structures of an elaborate system (Pl. 79, A).

As a result of such differences, the conidiophore top of the Visayan *Sclerospora* has a more spreading, expanded appearance; and the long axes of the branches, the sterigmata, and the conidia borne on them stand out from the main axis like rays of a partly opened fan. In *Sclerospora philippinensis*, on the contrary, the conidiophore top is more compact and less spreading, the axes of branches, sterigmata, and conidia being all approximately parallel to each other and to the main axis.

These differences in the conidiophores of the two fungi are, on the whole, relative rather than absolute and are influenced to some extent by such environmental conditions as the depth and persistence of the layer of dew in which they develop. Even these distinctions, however, could be used as more absolute and less relative criteria if a very large number of measurements of all parts of the conidiophores were made and assembled to give an adequate quantitative impression. Even from the qualitative rather than quantitative point of view, moreover, these differences, although relative, are constant and distinct, and it should be emphasized that they persist when the two fungi, developing under exactly parallel circumstances on sister plants of the same age, grown side by side under as nearly the same conditions of temperature, soil, dew deposition, etc., as it was possible to obtain, were compared by nightly examinations for several weeks.

CONIDIA.—Among the Peronosporaceae as a whole the characteristics of the conidia have been found to be the most valuable basis for distinguishing species. This applies equally well to these two *Sclerosporas*, since their conidia not only differ markedly and constantly in shape and size but also remain relatively unaffected by changes in environment and hosts.

In shape, the conidia of the Visayan *Sclerospora* are at once distinguished from those of *Sclerospora philippinensis*. They are not only much more elongate but much more slender as well, the length being frequently two or even three times the diameter. Consequently they range from very elongate ovoid and obovoidal bodies to long narrow, round-ended cylinders, but they are most commonly very elongately ellipsoid in shape. A clearer idea of these variations may be gained from Plate 79, I, J, K.

In such features as the rounded apex devoid of any papilla, the blunt base with its apiculus of attachment, the hyaline, granular content, and the thin wall, the conidia correspond to those of *Sclerospora*

*philippinensis*. As in the case of the latter species also, germination is invariably by the protrusion of one or more germ tubes (Pl. 79, I, J, K).

In size, the conidia of the Visayan *Sclerospora* are very variable. With respect to such widely varying bodies as the spores of this and other genera of Peronosporaceae, recent investigations have shown that it is no longer possible to delimit a species adequately by the extremes or averages of a few measurements. Rather, there is required the assembling and presentation in tables and graphs of a sufficiently large number of representative measurements to give a quantitative as well as a qualitative expression of the conidial characteristics of the species.

Accordingly, in order to obtain data adequate to identify the Visayan form and to furnish a basis for comparing it with others, 700 conidial measurements were made. These comprised measurement groups of 100 conidia from each of the two sugar-cane and the four *Saccharum spontaneum* plants from Cebu, and from one maize plant inoculated from the latter.

The conidia were taken from the leaves of the host at night during the optimum period of conidia production—from 2 to 4 a. m.—mounted in dew, and measured immediately.

Since, on examination, the seven measurement groups were found to agree in all essential particulars, they were combined into the total of 700. For the purposes of comparison, 700 measurements of *Sclerospora philippinensis* were secured in like manner.<sup>1</sup> Of these, 300 were new ones made of fresh conidia from teosinte and sorghum found infected in the college plots and from *Saccharum spontaneum* seedlings artificially inoculated from maize. All these groups were compared, found to agree, and grouped into the total of 700.

In making these measurements, care was taken to include every conidium in a marked area of the microscope field as the slide was moved along by the mechanical stage. Only those conidia obviously injured or those still attached to the conidiophores were excluded. The divisions of the eyepiece equaled approximately  $1.8\ \mu$ , and, with the magnification used, it was possible to estimate with fair accuracy to one-third of a division, or to about  $0.6\ \mu$ . Consequently, the measurements are exact to this extent—that is, the conidium recorded as  $32\ \mu$  in length may as well be  $31.4\ \mu$  or  $32.6\ \mu$  instead of exactly  $32\ \mu$  but not, in all probability,  $31$  or  $33\ \mu$ . With a large number of spores such differences tend to equalize themselves. As a result, the measurements presented here may be considered as adequately representing the characteristics of the conidia of the species involved.

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<sup>1</sup> The writer wishes to take this opportunity to call attention to an error in the tabulation of the previous spore measures of *Sclerospora philippinensis* (12, p. 110). In the table of length, the conidia measuring 41 to  $42.9\ \mu$  should be 23 in number instead of 24.

The measurements are summed up in Table I and are presented in graphic form in figure 1. In addition, the biometric characteristics of the two species are given in Table II. In making the calculations, the directions and formulae of E. Davenport (3) and C. B. Davenport (2)

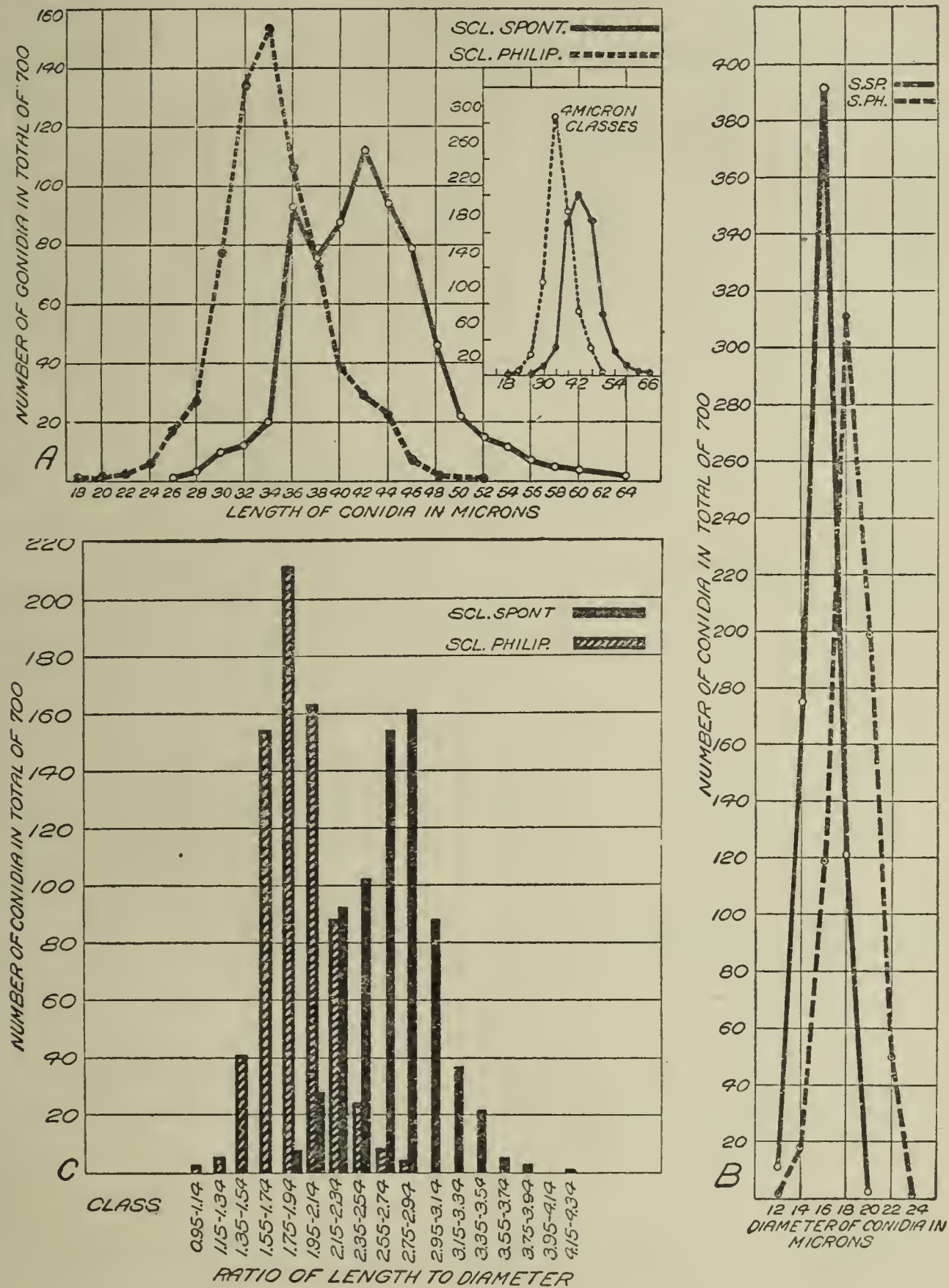


FIG. 1.—Comparison of the sizes of 700 conidia of *Sclerospora spontanea* with 700 conidia of *S. philippinensis*; A, variation of conidia in length; B, variation of conidia in diameter; C, ratios of length to width of conidia arranged in classes.

have been followed. The writer makes no pretense to a comprehensive biometric study of the two *Sclerosporas* but has used this method solely as a means to the end of presenting the accompanying data as a basis of comparison between these and other species.

TABLE I.—Summarized measurements of conidia of *Sclerospora spontanea* and *Sclerospora philippinensis*

| Length.       |                           |                           | Diameter.     |                           |                           | Length over diameter. |                           |                           |
|---------------|---------------------------|---------------------------|---------------|---------------------------|---------------------------|-----------------------|---------------------------|---------------------------|
| Classes.      | Number of conidia in 700. |                           | Classes.      | Number of conidia in 700. |                           | Ratio classes.        | Number of conidia in 700. |                           |
|               | <i>S. spontanea.</i>      | <i>S. philippinensis.</i> |               | <i>S. spontanea.</i>      | <i>S. philippinensis.</i> |                       | <i>S. spontanea.</i>      | <i>S. philippinensis.</i> |
| μ.            |                           |                           | μ.            |                           |                           |                       |                           |                           |
| 17 to 18.9... |                           | 1                         | 11 to 12.9... | 11                        | 2                         | 0.95 to 1.14...       |                           | 2                         |
| 19 to 20.9... |                           | 1                         | 13 to 14.9... | 175                       | 18                        | 1.15 to 1.34...       |                           | 5                         |
| 21 to 22.9... |                           | 2                         | 15 to 16.9... | 391                       | 119                       | 1.35 to 1.54...       |                           | 41                        |
| 23 to 24.9... |                           | 5                         | 17 to 18.9... | 121                       | 311                       | 1.55 to 1.74...       |                           | 154                       |
| 25 to 26.9... | 1                         | 17                        | 19 to 20.9... | 2                         | 199                       | 1.75 to 1.94...       | 7                         | 211                       |
| 27 to 28.9... | 3                         | 27                        | 21 to 22.9... |                           | 50                        | 1.95 to 2.14...       | 28                        | 163                       |
| 29 to 30.9... | 10                        | 77                        | 23 to 24.9... |                           | 1                         | 2.15 to 2.34...       | 92                        | 88                        |
| 31 to 32.9... | 12                        | 134                       |               |                           |                           | 2.35 to 2.54...       | 102                       | 24                        |
| 33 to 34.9... | 20                        | 153                       |               |                           |                           | 2.55 to 2.74...       | 154                       | 8                         |
| 35 to 36.9... | 93                        | 107                       |               |                           |                           | 2.75 to 2.94...       | 161                       | 4                         |
| 37 to 38.9... | 76                        | 75                        |               |                           |                           | 2.95 to 3.14...       | 88                        |                           |
| 39 to 40.9... | 87                        | 39                        |               |                           |                           | 3.15 to 3.34...       | 37                        |                           |
| 41 to 42.9... | 112                       | 29                        |               |                           |                           | 3.35 to 3.54...       | 22                        |                           |
| 43 to 44.9... | 94                        | 23                        |               |                           |                           | 3.55 to 3.74...       | 5                         |                           |
| 45 to 46.9... | 79                        | 7                         |               |                           |                           | 3.75 to 3.94...       | 3                         |                           |
| 47 to 48.9... | 46                        | 2                         |               |                           |                           | 3.95 to 4.14...       | 0                         |                           |
| 49 to 50.9... | 22                        | 0                         |               |                           |                           | 4.15 to 4.34...       | 1                         |                           |
| 51 to 52.9... | 15                        | 1                         |               |                           |                           |                       |                           |                           |
| 53 to 54.9... | 12                        |                           |               |                           |                           |                       |                           |                           |
| 55 to 56.9... | 7                         |                           |               |                           |                           |                       |                           |                           |
| 57 to 58.9... | 5                         |                           |               |                           |                           |                       |                           |                           |
| 59 to 60.9... | 4                         |                           |               |                           |                           |                       |                           |                           |
| 61 to 62.9... | 0                         |                           |               |                           |                           |                       |                           |                           |
| 63 to 64.9... | 2                         |                           |               |                           |                           |                       |                           |                           |

TABLE II.—Biometric constants of the conidia of *Sclerospora spontanea* and *Sclerospora philippinensis*

| LENGTH                      |             |             |                     |                     |                             |
|-----------------------------|-------------|-------------|---------------------|---------------------|-----------------------------|
| Species.                    | Mean.       | Median.     | Mode (approximate). | Standard deviation. | Coefficient of variability. |
|                             | μ.          | μ.          | μ.                  |                     |                             |
| <i>S. spontanea</i> .....   | 42.07±0.145 | 41.86±0.142 | 41.43               | 5.672±0.102         | 13.48±0.247                 |
| <i>S. philippinensis</i> .. | 34.52±.113  | 34.12±.142  | 33.32               | 4.439±.080          | 12.86±.235                  |
| DIAMETER                    |             |             |                     |                     |                             |
|                             | μ.          | μ.          | μ.                  |                     |                             |
| <i>S. spontanea</i> .....   | 15.79±0.036 | 15.84±0.045 | 15.93               | 1.395±0.025         | 8.83±0.160                  |
| <i>S. philippinensis</i> .. | 18.40±.047  | 18.36±.006  | 18.36               | 1.834±.033          | 9.97±.181                   |
| RATIO OF LENGTH TO DIAMETER |             |             |                     |                     |                             |
|                             |             |             |                     |                     |                             |
| <i>S. spontanea</i> .....   | 2.71±0.009  | 2.71±0.011  | 2.71                | 0.357±0.006         | 13.20±0.242                 |
| <i>S. philippinensis</i> .. | 1.91±.007   | 1.89±.008   | 1.85                | .266±.005           | 13.92±.256                  |

An examination of the data shows clearly that the long-spored Visayan form, *Sclerospora spontanea*, at least in regard to its conidia, is quite distinct from *S. philippinensis*. The location of the two frequency curves shows that the great bulk of the conidia of *S. philippinensis* fall between the limits of 31 to 36.9 μ in length, and 17 to 18.9 μ in width; while, on the contrary, a like proportion of those of *S. spontanea* are 37 to 46.9 μ in length and 15 to 16.9 μ in width. The somewhat irregular character

of the length curve of the latter species does not, in the opinion of the writer, indicate that it is bimodal, because, by using more inclusive measurement classes of 4  $\mu$  or even 3  $\mu$ , the depression so noticeable with the 2- $\mu$  classes smooths out and the curve becomes quite regular. Moreover, the difference between the modes as well as between the means and the medians is still sufficiently great to emphasize strikingly the dissimilarity in size of the conidia of the two species.

It should be noted that, although the curves of frequency distribution of the two species overlap slightly, size is none the less a valuable diagnostic criterion. In length, for instance, the curves overlap from 26  $\mu$ , the lowest limit of the Visayan Sclerospora, to 52  $\mu$ , the highest limit reached by *Sclerospora philippinensis*. As a result, it might be contended that size is of no value in distinguishing between the two species when applied at least to the conidia falling between these limits. While this is true of any one conidium, experience shows that, if several are measured, exceedingly few are to be found in this disputed region. For practical purposes even 50 unselected conidia of each species are sufficient to show the difference between them without any confusion due to overlapping.

It is also worthy of note that the curves of the frequency distribution of 700 conidia in both the Visayan species and *Sclerospora philippinensis* differ in no essential particular from those of 500, 400, or even as few as 200 conidia.

Furthermore, in the ratios of length to width of their conidia, the two species also show marked differences. The shorter, broader spores of *Sclerospora philippinensis* most commonly show ratios of 1.55 to 2.14, while in *S. spontanea* the greater length as well as the lesser width of the conidia is expressed by the predominant ratios of 2.35 to 2.94.

In order to determine whether the differences between the biometric characteristics of the two forms were indeed significant, the method quoted by Rosenbaum (11) from Reitz and Smith was employed. This method, which compares the difference between the mean or other constants with the probable error of the difference, shows that in *Sclerospora philippinensis* and *S. spontanea* these differences without doubt are significant and can not be the result of mere random sampling. This significance is clearly brought out in Table III.

TABLE III.—Difference in means of *Sclerospora spontanea* and *Sclerospora philippinensis* compared to the probable errors

| Difference in means.      |                           |                       | Difference in means divided by probable error of difference. |           |                       |
|---------------------------|---------------------------|-----------------------|--------------------------------------------------------------|-----------|-----------------------|
| Length.                   | Diameter.                 | Length over diameter. | Length.                                                      | Diameter. | Length over diameter. |
| $\mu$<br>7.55 $\pm$ 0.183 | $\mu$<br>2.61 $\pm$ 0.058 | 0.798 $\pm$ 0.011     | 41.27                                                        | 44.96     | 70.39                 |

The identity of the long-spored, Visayan *Sclerospora*, then, is clearly established as quite distinct from *Sclerospora philippinensis*. Whether this distinction is sufficient to entitle the former to specific rank depends somewhat upon the judgment of the investigator. The matter could be settled with greater finality if the two fungi were to be grown in pure culture and compared in morphological and physiological details under the controlled conditions of the laboratory, but unfortunately all attempts to grow the two forms artificially have been unsuccessful. In view, however, of such well-defined, although somewhat relative, morphological differences in the conidiophores as the peculiarities of the basal cell and the branch system, and the well-marked and easily measurable differences in size and shape between the conidia of the two fungi, and in view of the constancy and persistence of these points of dissimilarity over a wide range of hosts, through several generations of maize and during three months' cultivation, the writer regards the Visayan form as worthy of specific distinction from *S. philippinensis*. The species, therefore, is described as new, and as it was first found occurring spontaneously on a wild host, it is named *S. spontanea*.

#### DIAGNOSIS

##### *Sclerospora spontanea*, n. sp.

Symptoms, effect on the individual host, and destructiveness to the maize crop as a whole, as previously described by the writer for *Sclerospora philippinensis* (12).

Mycelial hyphae and haustoria as described for *Sclerospora philippinensis*; but the clavate hyphae (conidiophore initials) which emerge from the stomata are longer, more slender, and more irregular.

Conidiophores as in *Sclerospora philippinensis*, erect, single or grouped, developing only at night and in dew; comprising basal cell, main axis, more or less complex dichotomous branching system, and terminal sterigmata; but differing in general in greater total length (350 to 550  $\mu$ ) and more expanded top, and in particular as follows: Basal cell less knobbed and expanded at the base, more slender (least diameter about 5 to 8  $\mu$ ), and longer (140 to 260  $\mu$ ), usually exceeding or at least equaling in length the extent of the main axis from the septum to the primary branches. Main axis usually expanding more abruptly above the septum to a greater width (22 to 32  $\mu$ ) and constricting noticeably (to about 20  $\mu$ ) below the branches. Branches longer, more slender, less constricted at point of origin, less recurved and ascending, but standing out more stiffly. Sterigmata longer (13  $\mu$ ), more slender, and straighter.

Conidia resembling those of *Sclerospora philippinensis* in hyaline, finely granular content, thin wall, rounded apex lacking papilla, and rounded base with apiculus of attachment, and in invariable germination by tubes; but differing as follows: In shape, longer and more slender, usually very elongately ellipsoid or cylindrical; in size, showing greater length and less width, the majority being 39 to 45  $\mu$  long by 15 to 17  $\mu$  in diameter.

Oospores not yet encountered on maize, although an oogonial stage on *Saccharum spontaneum* may prove to be connected.

HABITAT.—Found in the Visayan group of the Philippine Islands principally on cultivated maize (*Zea mays* L.), rarely on the wild grass bugan̄ (*Saccharum spontaneum* L.), and once on cultivated sugar cane (*Saccharum officinarum* L.). Inoculated successfully upon the first two of these hosts and also upon teosinte (*Euchlaena luxurians* Schrad.), and the wild grass *Miscanthus japonicus* (Thunb.) Anders. Extremely destructive to maize, but much less so to the other hosts.

Material of the type will be found in the pathologic collections of the Bureau of Plant Industry, Washington, D. C., and in the herbarium of the Bureau of Science, Manila, P. I.

#### DISCUSSION

##### RELATIONSHIP

The two *Sclerosporas*, *Sclerospora spontanea* and *S. philippinensis*, are undoubtedly closely allied to each other. It is even possible that future investigation will bring to light forms intermediate between them. Such may be the downy mildew on maize seen by Prof. Reinking in the Cotabato Valley and by Gov. Coverston in Lanao Province, both of which places are in the southern Island of Mindanao. On the other hand, the Mindanao form may be as different from *S. spontanea* and *S. philippinensis* as these have proved to be from each other. The writer feels confident that on further search additional *Sclerosporas* will be encountered in the Philippines both on cultivated hosts and on wild grasses.

The relationship of the Philippine downy mildew *Sclerospora* to the similar forms described on maize and related crops from other oriental countries has been discussed in connection with *Sclerospora philippinensis* (12). Unfortunately the matter can not be settled finally with the data available. As the writer's discovery that suitable material can be secured only at night is very recent, previous publications present measurements and other data inadequate for comparison with living material. In so far as one can judge, however, *S. spontanea*, on account of its longer, more slender spores, is even more sharply distinguished than is *S. philippinensis* from the Javan species, *S. javanica* Palm (10), from the species of British India, *S. maydis* (Rac.) Butl. (1), and from the normal, short-spored type of the Formosan species, *S. sacchari* Miyake (9). It is of interest to note, however, that in the greater length of its conidia, the very character wherein it differs so distinctly from these other oriental species, *S. spontanea* tends to resemble the two abnormally long-spored forms recorded by Japanese investigators. In his account of *S. graminicola*, Ideta (8, p. 143-145), in addition to conidia of the size characteristic of the species, mentions a class of conidia having the—

shape of a long ellipse, 38.4 to 57.6  $\mu$  long by 19.2 to 24  $\mu$  wide.

Also, Miyake (9), in his account of *S. sacchari*, describes conidia not only of the usual shape and size, but also of an unusual type—

long ovate, 49 to 54  $\mu$  by 19 to 23  $\mu$ .

The descriptions and drawings of both these long types of conidia remind one of the spores of *S. spontanea*, even though the latter are characteristically more slender. It is very probable that the occurrence of these long conidial types in Japan and in Formosa indicates the

existence there of strains or species of *Sclerospora* as yet unrecognized; but what their relationship and significance may be, future investigation must determine.

The relationship of these two Philippine conidial forms to the oogonial stage characteristic of the genus is as yet unknown. Whether *Sclerospora philippinensis* or *Sclerospora spontanea* is connected with the oogonia stage which is so common on *Saccharum spontaneum* throughout the Philippine Islands is yet to be established. The writer has attempted to germinate the oogonia of the latter and to obtain inoculations with them, but so far he has been unsuccessful. Until the precise connection is definitely established, it is well to be cautious about assuming that the two types of spores are with certainty different phases of the same species. It may be worthy of note that the writer has found, in addition to the oogonia on *Saccharum spontaneum*, similar spores on *Miscanthus japonicus* and on cultivated sugar cane in the mountains of northern Luzon. On all these hosts the oogonia are apparently the same species; and their significance and importance will be discussed by the writer in a later paper.

#### NONSPECIALIZATION

As the problem now stands, the Philippine maize-mildew presents an interesting situation, since it involves two causal *Sclerosporas* quite distinct morphologically but practically indistinguishable physiologically both in their effect on, and in their virulence to, a range of hosts. The genus *Sclerospora* seems, then, to present a marked contrast to the strong specialization of the closely related genus *Peronospora*. In the latter, the work of Gäumann (5, 6, 7) has shown that the species are strongly specialized, being distinct on different hosts. This is true especially in the Rubiaceae (7), but also to a marked degree in the Cruciferae (5) and the Scrophulariaceae (6). The distinction holds both morphologically, in the size and character of the conidiophores and conidia, and also physiologically, in their inability to infect any host species but that from which the spores were derived. Gäumann, therefore, regards it as highly improbable that the same host species would be found to harbor more than one species of *Peronospora*. In *Sclerospora*, however, we have the two species, *Sclerospora spontanea* and *S. philippinensis*, morphologically distinct, yet both with equal ease inoculating the same series of hosts, including members not only of the Maydeae but also of the Andropogoneae.

#### SIGNIFICANCE OF OCCURRENCE

The finding of *Sclerospora spontanea* on a wild gramineous host is of interest. Hitherto in spite of the attention which the destructive oriental *Sclerosporas* have attracted, no conidial representative of the genus has ever been reported as occurring naturally upon a wild host. It is a question whether the occurrence of *Sclerospora spontanea* on wild

*Saccharum* in the Visayan Islands should be regarded as throwing light on the problem of the origin of the Philippine downy mildews of maize. In the opinion of the writer this and other facts indicate that the native grasses of the Philippines were the original hosts from which the downy mildews passed and are passing to such very susceptible introduced crops as maize. On the other hand, one should not overlook the possibility that the wild *Saccharum* clumps might have been infected with the downy mildew from badly diseased maize growing near. In this connection it should be noted that in two cases where *Sclerospora spontanea* was found on wild bugañ grass (*Saccharum spontaneum*) the infected clumps were so far distant and so protected from any downy-mildewed maize that there was little possibility of their having been infected thus. In the other cases the infected bugañ clumps were much older than the mildewed maize adjacent; and, because inoculation experiments have shown that bugañ grass is susceptible only as comparatively young seedlings, there is little doubt that the infection in the grass clump had been carried over in the perennial rootstocks and had not been caught from maize.

Moreover, it is worthy of note, also, that the wild *Saccharum* is very resistant to the effect of the *Sclerospora*, while maize is exceedingly unresistant. In contrast to the susceptibility to severe injury already noted in maize, wild *Saccharum*, even though heavily infected, shows only slight striping of the leaves (Pl. 78, B, C), remains undeformed, and is not materially retarded in development. In spite of the downy mildew the plants continue to grow vegetatively, to produce flowers (Pl. 77, B), and to form, by tillering, dense clumps which by extensive rootstocks persist from season to season, still supporting the active and equally persistent parasite. Because, as a rule, it is the introduced host which is most injured by a disease and the original, native host which is relatively unaffected, the indications are that wild *Saccharum* and not maize is the original host of *Sclerospora spontanea*.

The finding of *Sclerospora spontanea* on sugar cane is a second point of interest. Because, in Formosa, the closely related species *S. sacchari* Miyake had proved indiscriminately destructive to both sugar cane and maize, the writer, while in the Philippines, made especial effort to discover instances of the transmission of downy mildew from one to the other of these hosts. The single case in Cebu, however, was the only one noted. In this instance the single clump of sugar cane infected with *S. spontanea* was situated at the extreme edge of the field, separated only by a narrow trail from a large planting of badly downy-mildewed maize. Although the whole sugar-cane field was carefully inspected, no other cases of *Sclerospora* were discovered. It is natural to infer that the sugar-cane plant was infected from the neighboring maize, especially since the two parasites proved to be the same. It is rather surprising, however, that this lone cane plant, of all the thousands examined in scores of different

fields adjacent to or even interplanted with infected maize, should be the only one to succumb.

The matter is still further complicated by the fact that in Formosa Miyake easily obtained the infection of sugar-cane plants grown from cuttings, while in the Philippines the writer was not able to inoculate cutting-grown plants of sugar cane, or even of *Saccharum spontaneum*, although seedlings of this grass were readily infected (Pl. 78, A). Moreover, in Formosa the effect of *Sclerospora sacchari* Miyake on sugar cane is far more destructive than was the effect of *Sclerospora spontanea* on this single cane plant. In the former the elongation and weakening of the shoots and the conspicuous yellowish striping of the leaves are a distinct contrast to the stunting of the shoots and faint, pale green markings of the leaves which characterized the Philippine specimens. Also, although the latter died shortly after being transplanted, this was apparently due to the severe treatment they had received rather than to the destructive character of the *Sclerospora*. It is possible that *Sclerospora spontanea*, in its essential individuality, is much less virulent to sugar cane than *Sclerospora sacchari*, or it may be that some limiting factor is operative in the Philippines. The work of Fawcett (4) indicates that temperature differences may exercise an important limiting effect within a smaller geographic range than from Cebu to Formosa. In any case, although the matter is in need of further study, it can safely be said that in so far as has been observed in the Philippines the production of sugar cane is unaffected by *Sclerospora spontanea* or other conidial *Sclerosporas*.

#### SUMMARY

The downy mildew of maize which is extremely destructive in the Philippine Islands has been found to be caused by the Peronosporaceous genus *Sclerospora*. At first only one species was thought to be involved, and this was described by the writer as *Sclerospora philippinensis*. More recently the problem presented by the Philippine maize-mildew has been still further complicated, since a second causal species of *Sclerospora* has been found to be concerned also. The foregoing paper describes this species as new (*S. spontanea*) and presents briefly its morphological and physiological characteristics and its importance and relationship.

*Sclerospora spontanea*, the more recently discovered form, occurs in the Islands of Cebu, Bohol, and Leyte, where it was found on the wild grass *Saccharum spontaneum* L., on sugar cane (*Saccharum officinarum* L.), and on maize (*Zea mays* L.). *Sclerospora philippinensis*, the species first recognized, occurs in the Island of Luzon, where it was found on maize, teosinte (*Euchlaena luxurians* Schrad.), and sorghum (*Andropogon sorghum* [L.] Brot.).

Morphologically, *Sclerospora spontanea* is characterized by the relatively much greater length and slenderness of its conidiophores in general and of its basal cells and conidia in particular. In these respects it differs markedly from *S. philippinensis*, which has shorter, stockier

conidiophores, shorter, thicker basal cells, and shorter, broader conidia. There are, moreover, some minor distinctions between the branch systems and between the sterigmata of the two species.

These differences remain constant for each species and are not influenced by growth on different hosts even through several generations. Both species have been artificially inoculated with equal ease from one to another of the following hosts: Maize, teosinte, *Miscanthus japonicus*, and *Saccharum spontaneum*. Attempts to inoculate sorghum artificially were unsuccessful with both species. Because no seedlings of sugar cane were available, no inoculation with either fungus was attempted. Inoculations on sprouted sugar-cane cuttings were uniformly unsuccessful.

Since the size and shape of the conidia are the most useful criteria of interspecies distinction, they are given in detail. Measurements of 700 conidia of each of the two species were combined into comparative tables and graphs of frequency distribution in an attempt to present the differences between them quantitatively as well as qualitatively.

Although morphologically the two species differ as has been described, yet physiologically, in general effect in the field, in effect on the individual plant, and in virulence to the same wide range of hosts no distinction between them is apparent.

The discovery that two forms are involved complicates the problem presented by the Philippine downy mildew of maize. Because two forms morphologically different but practically indistinguishable in physiologic effect are concerned in the same disease, there appears to be a decided lack of that specialization which characterizes certain other genera of the Peronosporaceae. It seems highly probable that still other forms will be found to be concerned in similar diseases in the Philippine Islands and throughout the Orient.

In addition to these two conidial species with a host range of maize, teosinte, sorghum, sugar cane, *Saccharum spontaneum*, and *Miscanthus japonicus*, the writer has encountered in the Philippines oogonial stages of *Sclerospora* on *Saccharum spontaneum*, *Saccharum officinarum*, and *M. japonicus*. The oogonia on these three hosts are practically indistinguishable. Whether these oogonial and conidial stages are quite unrelated or are indeed only phases in the development of the same organism remains to be determined.

*Sclerospora spontanea*, like *S. philippinensis*, is closely related to the other conspicuous conidial *Sclerosporas* of the Orient: *S. javanica* Palm, of Java; *S. maydis* (Rac.) But., of India; and *S. sacchari* T. Miyake, of Formosa. All these forms are characterized by the predominance of the conidial stage, the absence or great rarity of the oogonia, germination of the conidia by tubes, and the occurrence on maize, sugar cane, and related hosts in the Orient. *S. spontanea*, however, because of its longer, more slender spores is as a species distinguished even more sharply than *S. philippinensis* from these other oriental representatives.

The discovery of *Sclerospora spontanea* on wild *Saccharum spontaneum* is, in so far as the writer is aware, the first record of the occurrence of a conidial *Sclerospora* on a wild host in the Orient. This occurrence, in connection with other data, seems to the writer to indicate that the wild grasses are the natural hosts of these oriental downy mildews from which they have passed and are passing to susceptible introduced crops such as maize.

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PLATE 76<sup>1</sup>

Corner of a native-grown maize plot in the interior uplands of Cebu. At the edge of this field, in which many maize plants were being killed by downy mildew, were occasional clumps of the wild grass (*Saccharum spontaneum* L.) called "buganġ" in the Visayan Islands. One of these clumps, which was severely infected with *Sclerospora spontanea*, is shown at the left. The older, primary stalk of this clump, had died, but although the remaining shoots were apparently uninjured, great numbers of conidiophores were being produced on them, especially on the one held out for inspection. The base of this shoot was a few feet farther down the steep slope at the point indicated by the arrow. Behind the central figure can be seen a maize plant noticeably discolored by the downy mildew.

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<sup>1</sup> Photographs by W. H. Weston.





PLATE 77

A.—Clump of *Saccharum spontaneum*, showing characteristic size and habit of healthy plants under natural conditions. The measure is 2 meters tall.

B.—Clump of *Saccharum spontaneum* infected with *Sclerospora spontanea*. When transplanted to this container in Cebu the infected plant comprised a single shoot separated from the clump shown in the preceding plate. This shoot continued to develop vigorously in spite of the downy mildew until after  $5\frac{1}{2}$  months it had produced the thriving clump shown. Conidiophores were still being produced in abundance, especially by the younger stalks. Same measure as in A.

PLATE 78

A.—A young seedling (3 weeks old) of *Saccharum spontaneum* infected with *Sclerospora spontanea*. On this seedling, which was artificially inoculated on the second night after it emerged, conidium production began on the sixth night following and recurred in increasing abundance on successive nights. In contrast to healthy seedlings this plant betrays the effect of the *Sclerospora* in its pallor and in the presence of a whitish "down" of conidiophores. These have collapsed on drying but can still be seen on that part of the fourth leaf indicated by the pointer.  $\times \frac{3}{4}$ .

B.—Conidiophores on the leaf of *Saccharum spontaneum*. A portion of the upper leaf surface of a downy-mildewed plant (Pl. 77, B) showing remains of the whitish "down" of innumerable conidiophores produced during the night. Although photographed as early as light would permit, the leaf surface has dried somewhat and the fragile conidiophores have shrunk and matted together.  $\times 1\frac{1}{2}$ .

C.—Young shoots of *Saccharum spontaneum* arising after the primary stalk had been cut, and like it severely infected with *Sclerospora spontanea*. The main plant, one of the four downy-mildewed ones transplanted from Cebu, was cut off close to the ground. All the subsequent shoots arising from the remaining base were, from the first leaf, badly infected with *Sclerospora* and produced abundant conidiophores.

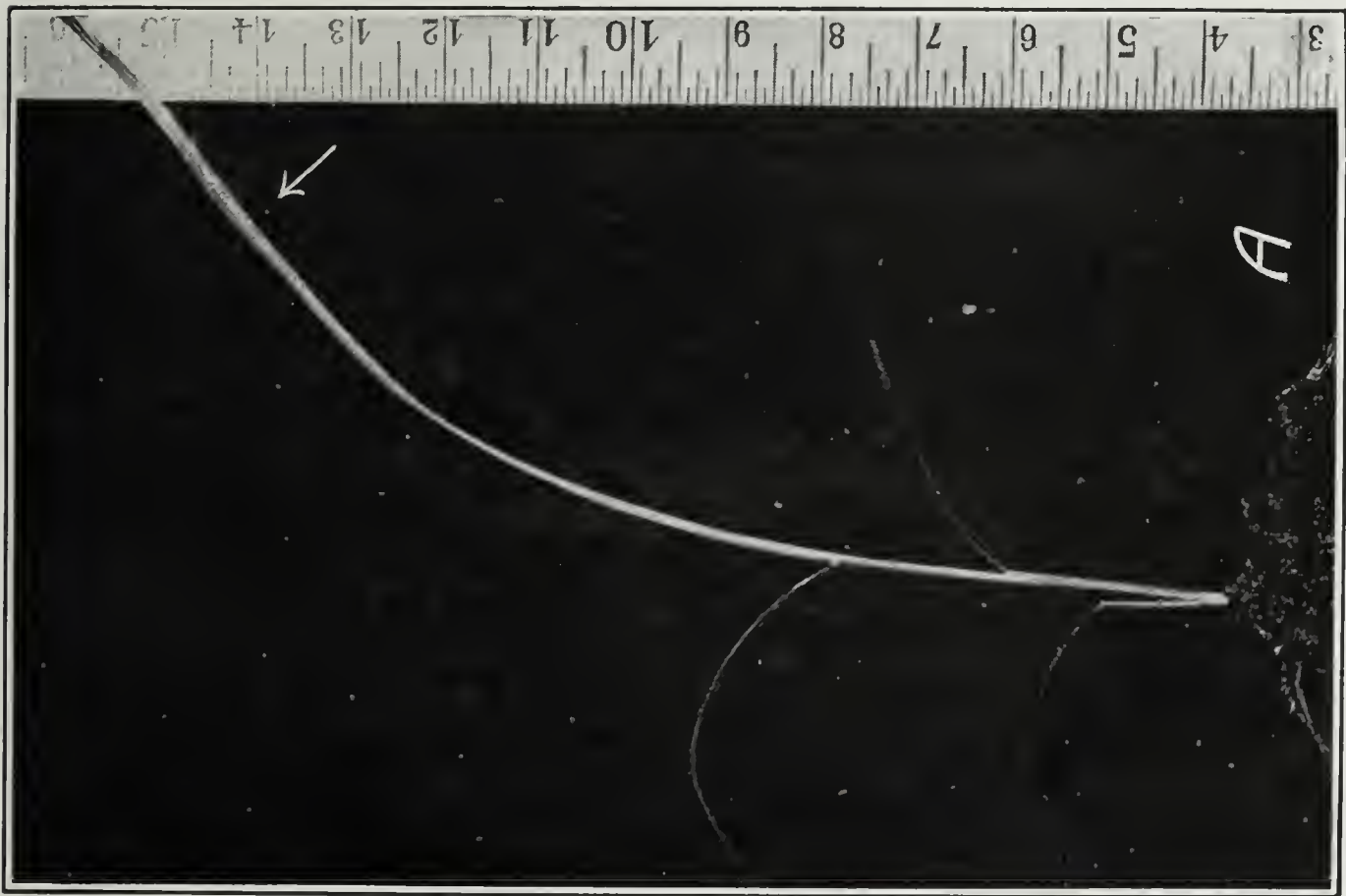
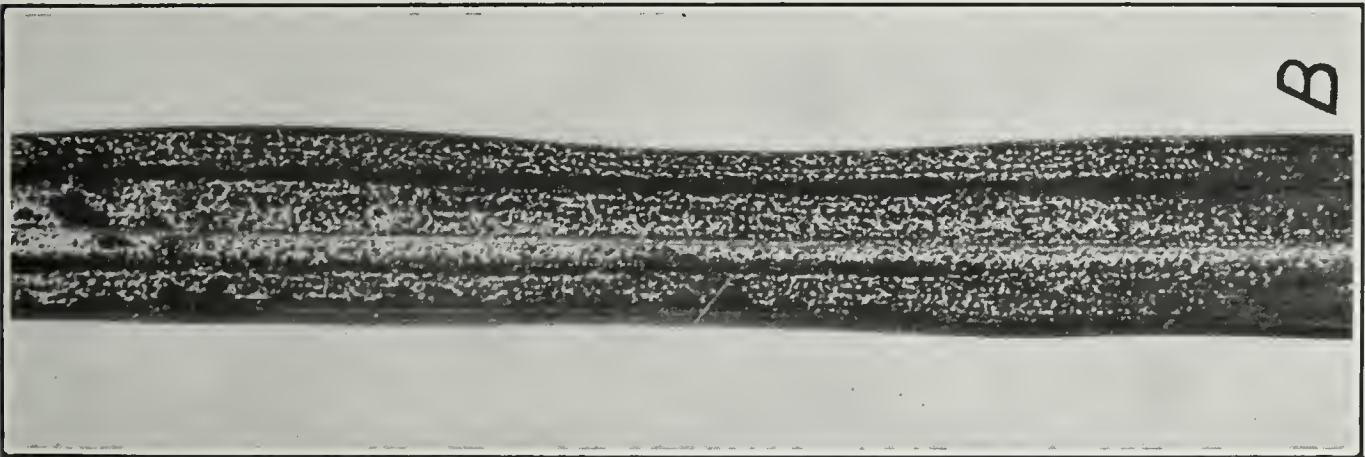
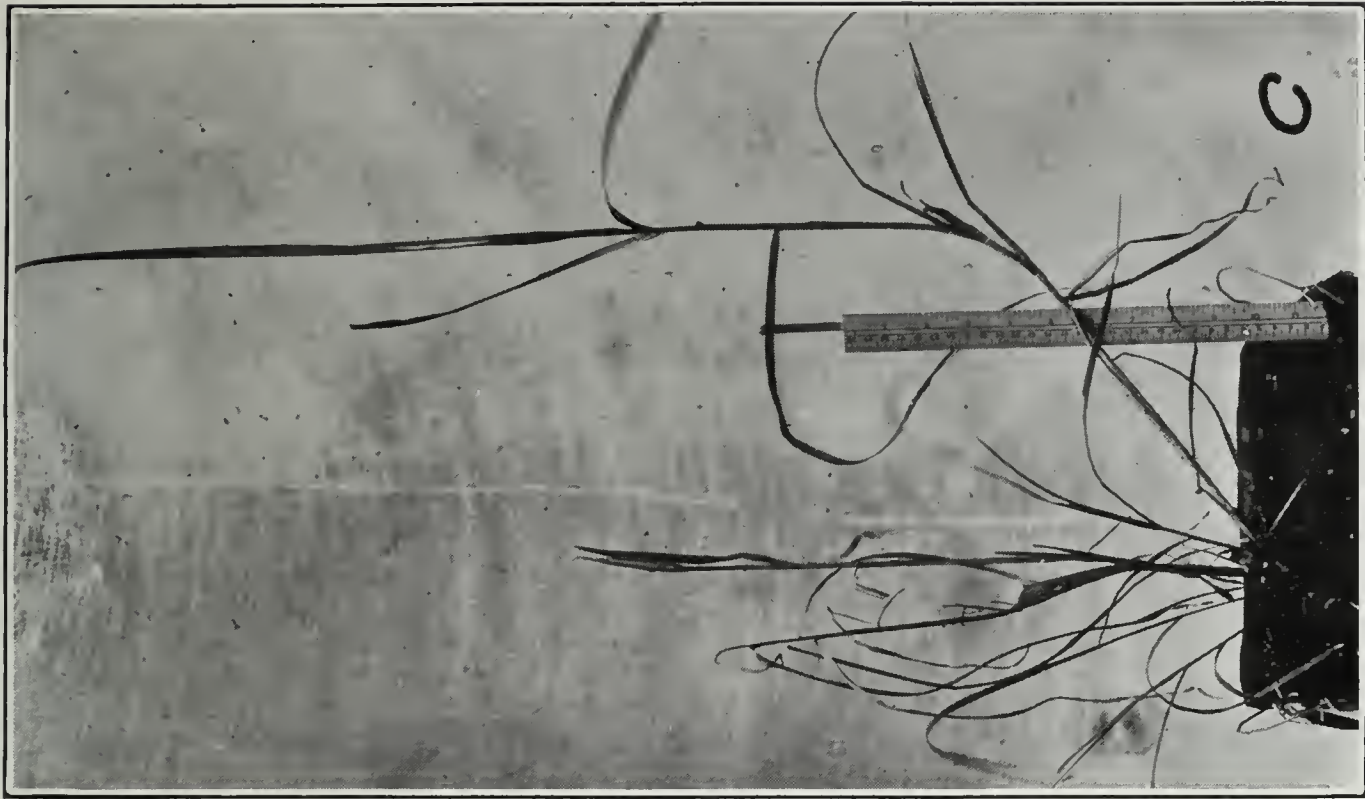




PLATE 79<sup>1</sup>

A.—Typical conidiophore,<sup>2</sup> showing characteristically long, slender, unknobbed basal cell, relatively short main axis with its greatest diameter about midway to the primary branches, and fairly well-developed branch system bearing long, slender conidia. The number of conidia is somewhat less than that usually encountered. From maize inoculated from *Saccharum spontaneum*.  $\times 375$ .

B.—Upper portion of a conidiophore which has a poorly developed branch system and hence bears few conidia on sterigmata which are relatively large. Several conidia have been broken off in mounting. From maize.  $\times 375$ .

C.—Portion of the branch system of a conidiophore, showing the conidia germinating while still attached to their sterigmata. From maize.  $\times 375$ .

D.—Stalk portion of a typical conidiophore, showing long, slender, unknobbed basal cell, and main axis which is slender above the septum, expands rapidly to its greatest diameter about midway, and contracts again below the branches. From *Saccharum spontaneum*.  $\times 375$ .

E, F.—Typical basal cells of conidiophores. E from *Saccharum spontaneum*; F from sugar cane.  $\times 375$ .

G.—Stalk portion of a conidiophore with basal cell which, though unusually short, nevertheless is longer than the extent of the main axis from septum to primary branches. From *Saccharum spontaneum*.  $\times 375$ .

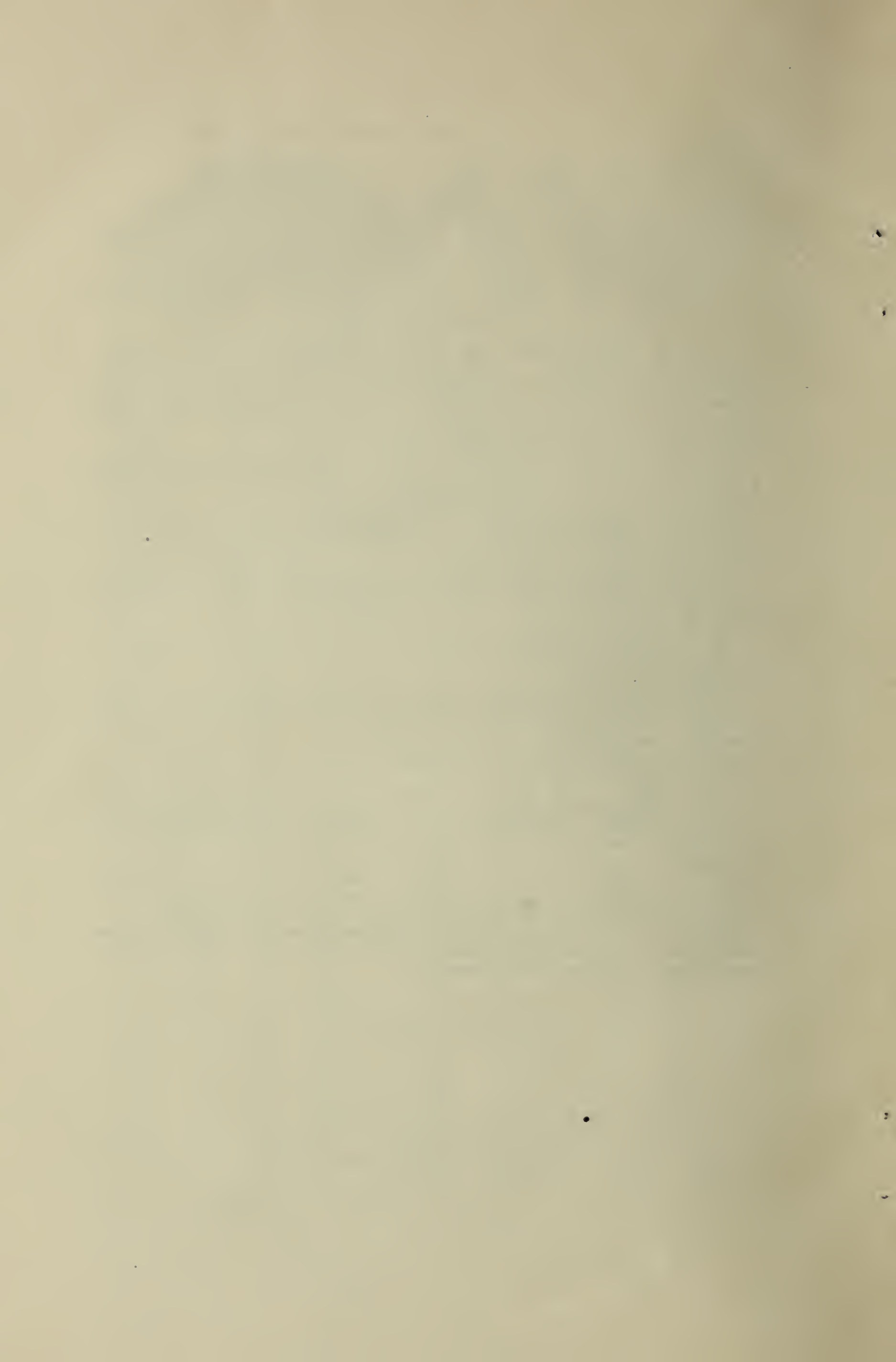
H.—Typical stalk portion of a conidiophore from sugar cane. Compare with A and D.  $\times 375$ .

I, J, K.—Typical conidia showing variations in size and shape and method of germination by hyphae. I from maize, the lowest figure from material especially fixed and stained to bring out the internal structure; J from *Saccharum spontaneum*; K from sugar cane.  $\times 375$ .

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<sup>1</sup>The drawings were made with the aid of a camera lucida. Figure A and the ungerminated conidia of figures I, J, and K are from fresh material. All the other drawings are from preserved specimens.

<sup>2</sup>In comparing these drawings with the plates of *Sclerospora philippinensis* (12) it should be noted that the latter give a somewhat misleading impression of the relative spreading of the branch system because the conidiophores were flattened slightly in mounting.











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